STUDIES ON WATER RELATIONS IN FLORIDA TERMITES
I. SURVIVAL TIME AND RATE OF WATER LOSS DURING DRYING

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Introduction

Species differences in tolerance of drying have been established in four members of the genus *Reticulitermes* (Williams, 1934, and Strickland, 1950). Caste differences in rate of loss and survival time during drying have been described in *Reticulitermes flavipes* (Kollar) by Dunmore and Collins (1951). In an attempt to determine the factors influencing rate of loss and survival time during desiccation, studies of water relations in termites were extended to include 9 of the 13 species of termites found in Florida.

Material

The termite fauna of Florida includes species distributed among the three major habitat types, subterranean, damp-wood, and dry-wood. The following listed species, with ranges and environmental moisture requirements as described by Miller (1949), were utilized in the study:

1. *Kalotermes jouteli* Banks, a large dry-wood termite limited largely to coastal zones of southern Florida, requiring more moisture than other species of the genus.
2. *Kalotermes schwarzi* Banks, similar to *K. jouteli,* but with a wider range.
3. *Kalotermes snyderi* Light, a species ranging inland and through north Florida, with a smaller moisture requirement than either *jouteli* or *schwarzi.*
4. *Cryptotermes cavifrons* Banks, a small dry-wood termite probably indigenous to Florida.
5. *Cryptotermes brevis* (Walker), seemingly an introduced species living in furniture and houses, and not yet reported from natural habitats.

6. *Neotermes castaneus* (Burmeister), the largest termite found in Florida, limited to damp wood or dead branches on living trees, ranging southward from Vero Beach.
7. *Reticulitermes hageni* Banks, the smallest species of the subterranean termites.
8. *Reticulitermes virginicus* Banks, an intermediate-sized species.
9. *Reticulitermes flavipes* (Kollar), the largest and most widely distributed species of the genus.

Field observations and reports from exterminating companies suggest that of the three species of subterranean termites, *R. hageni* has the lowest moisture requirement, *R. virginicus* is intermediate, and *R. flavipes* has the highest (Miller, 1949). All three *Reticulitermes* species are dependent upon a constant moisture supply, however, and this is usually obtained through soil contact. Unlike *Neotermes* and the dry-wood termites, *Reticulitermes* species do not form faecal pellets, but void a liquid excrement that is utilized in construction of galleries or ingested by other members of the colony. Desiccating specimens may occasionally show a plug of dry material protruding from the anus, but under culture in the laboratory or in the field, such pellets are not observed. In the dry-wood and damp-wood termites, water is extracted from the digestive wastes and a dry firm pellet is voided.

Methods

Termites were collected in the Everglades National Park, the Florida Keys, the University of Miami South Campus, the greater Miami area, the Highlands Hammock State Park, and the Tallahassee area.

Maintenance of colonies of species with a high moisture requirement was achieved by placing the termites in finger bowls containing a ½ inch layer of a stiff solution of agar and sawdust.

Wood containing colonies of dry-wood termites was broken into small sections and placed in dressing jars. Lumps of agar-sawdust mixture were added when the termites showed signs of becoming desiccated.

Furniture termites were left undisturbed until needed. After colonies had been entered and experimental animals removed, some of the wood and the remaining termites were transferred to dressing jars. Agar-sawdust lumps were quickly utilized by *C. brevis* in forming enclosed cells between adjacent pieces of wood.

Ant attacks were prevented by surrounding the dressing jars with water or coating them with vaseline.

Rate of water loss of living specimens was determined by weighing groups of termites, exposing them to air of 0-4 per cent relative humidity for measured intervals of time, and determining the weight after exposure. The hourly rate of loss of individuals was computed by dividing the total weight lost by the group by the number in the group and the hours of exposure. Rate determinations were calculated on the basis of loss of body weight at the fourth hour of drying. No corrections were attempted for weight changes due to gain of O_2 or loss of CO_2. Gunn (1934) found that weight changes due to respiratory exchange had an upper limit of 10 per cent of the total loss in the cockroach, and stated that the rate of total loss could be taken as a satisfactory measure of the rate of water loss.

Weight determinations were made with a Becker Chain-O-Matic balance of 1/20 mg. sensitivity.

Indicating Drierite (anhydrous calcium sulphate with cobalt chloride) was the desiccant employed.

Four samples were run concurrently in most experiments. The number of termites used in a sample varied with size, species, and the number available.

Care was exercised to avoid jolting the weighing bottles containing the termites as far as was possible, as members of some species will evacuate the gut at a disturbance. It is probable that this source of error is partly involved in the variability between samples. It can be excluded by killing the termites before desiccating them.

Death could not be determined precisely, so an end point was chosen. Absence of observable movement after slight displacement was taken to indicate death.

Observations and Results

The results are summarized in Tables I, II, III, IV, V, and VI, and Figure I.

TABLE I

CASTES, SAMPLE SIZE AND NUMBER, WEIGHT, RATE OF LOSS, AND SURVIVAL RANGES

Species, Castes	No. of Samples	No./ Sample	Range, Sample Wgts, (Mg)	Range, Individual Wgts. (Mg)	Range, Rate of Loss Mg/Termite/Hr First Four Hours	Range, Av. Survival Time (Min. or days)
R. hageni — W., S.	5	25	26.0– 31.0	1.04– 1.24	.133–.174	240–297 Min.
R. virginicus — W., S.	4	30	74.2– 78.5	2.47– 2.70	.161–.217	360–376 min.
— Im. nymphs	1	25	73.7	2.94	.192	374 min.
— Im. nymphs	2	20	47.6– 48.5	2.38– 2.42	.102–.150	342–390 min.
— Im. 1-2 days	1	20	46.5	2.32	.235	288 min.
— Im. Old	1	20	40.0	2.00	.172	258 min.
R. flavipes — W.	1	20	58.5	2.92	.287	336 min.
— W., S.	7	25	63.5– 72.5	2.54– 2.90	.214–.302	259–374 min.
— Dry Agar, W., S.	1	25	72.0	2.88	.307	182 min.
— N., W., S., Sec. Sex.	1	25	73.4	2.93	.167	Not observed
— N., W., S.	2	20	63.2– 68.0	3.16– 3.40	.200–.265	Not observed
— Im, 1–3	1	20	89.1	4.45	.290	354 min.
C. cavifrons — Wet N	2	22	71.2– 71.3	3.23– 3.24	.036–.042	No deaths
— Wet N	1	10	39.6	3.96	.04	———
— Dry N	3	20	53.7– 80.5	2.68– 4.02	.009–.022	———

Table I (Continued)

C. brevis	— N	5	10	58.0– 85.4	5.80– 8.54	.000–.050	1 death, probably injured
	— N	1	15	91.8	6.12	.003	
	— Im.	1	15	61.0	4.06	.015	————
K. snyderi	— N., S.	2	8	67.2– 85.0	8.4 –10.6	.041–.062	< ½ dead: 22 days
	— N	1	8	73.0	9.1	.062	
	— N	4	10	78.7–105.7	7.87–10.57	.020–.097	
K. schwarzi	— N	4	10	88.8–119.5	8.88–11.95	.045–.090	11.6 days
K. jouteli	— Wet N	5	10	80.7–110.4	8.07–11.04	.09 –.19	4+ days
	— Dry N	3	10	149.5–222.2	14.95–22.21	.052–.090	12+ days
	— Dry N	2	4	55.0– 83.0	13.75–20.7	.056–.093	
	— Dry Im.	2	4	61.6– 70.5	15.4 –17.6	.156–.162	
N. castaneus	— 1st run N	6	10	95.5–150.2	9.55–15.02	.210–.367	3+ days
	— 2nd run N	2	10	92.3– 95.7	9.23– 9.57	.182 (both groups)	

W = Workers
Im. = Imagoes
N. = Nymphs
S. = Soldiers
Sec. Sex. = Secondary Reproductives

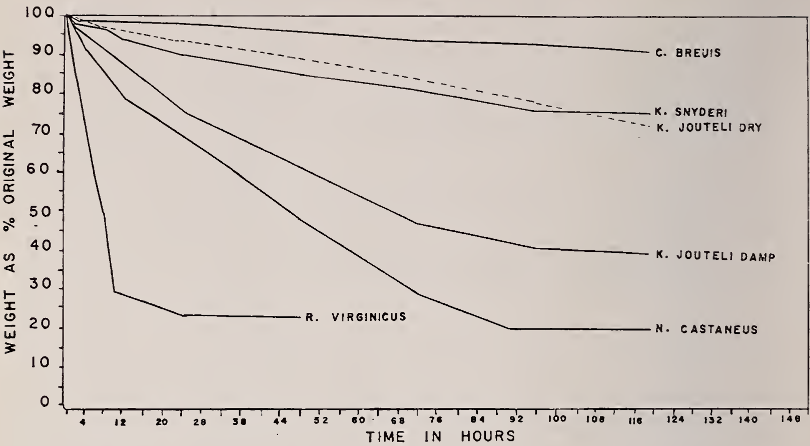

Figure 1. Percentage of body weight remaining at intervals during desiccation (2-120 hours).

Rate of loss decreased with time in species except *Cryptotermes* (*brevis* and *cavifrons* cultured dry), where the initial rate was low and remained low unless a member of the group showed signs of injury. The rate decrease was pronounced in dry-wood termites cultured under moist conditions.

TABLE II

RATE OF LOSS EXPRESSED AS MG/TERMITE/HOUR
DATA ON W, S, N GROUPS—FIRST FOUR HOURS OF DRYING

Species	Average Rate of Loss ± S. E.	σ
Reticulitermes flavipes	.260 ± .013	.0460
Neotermes castaneus — 1st run	.251 ± .027	.0608
— 2nd run	.182	
Reticulitermes virginicus	.178 ± .019	.0480
Reticulitermes hageni	.155 ± .029	.0580
Kalotermes jouteli—wet	.149 ± .019	.0340
Kalotermes jouteli—dry	.070 ± .024	.0540
Kalotermes schwarzi	.066 ± .009	.0180
Kalotermes snyderi	.052 ± .010	.0230
Cryptotermes cavifrons—wet	.039 ± .002	.0030
Cryptotermes cavifrons—dry	.016 ± .004	.0069
Cryptotermes brevis	.015 ± .007	.0192

Imagoes were more active than nymphs dring desiccation, and subterranean termites were more active than the dry-wood or furniture termites. The latter groups tended to "huddle", and remain motionless until the desiccator was opened for observation.

TABLE III

STATISTICAL COMPARISONS BETWEEN SPECIES LISTED IN TABLE II (RATIO OF DIFFERENCE, D, TO THE STANDARD ERROR OF THE DIFFERENCE σD)

Species Compared	$D/\sigma D$	P
R. flavipes / R. virginicus	3.5	$< .003$
R. virginicus / R. hageni	$D<\sigma D$	
R. hageni / R. flavipes	3.2	$< .003$
R. flavipes / N. castaneus	$D<\sigma D$	
K. jouteli wet / K. jouteli dry	3.95	$< .003$
R. hageni / K. jouteli dry	2.83	$< .005$
R. hageni / K. jouteli wet	$D<\sigma D$	
C. cavifrons wet / C. cavifrons dry	9.2	$< .00001$
C. cavifrons dry / C. brevis	$D<\sigma D$	
C. brevis / K. snyderi	3.0	.003

Deaths in dry-wood termites (*Kalotermes* species) were widely separated. It appeared that an individual in the group would be drained of fluid, then another, and so on until only one or two were active. These would look normal long after the others had become much flattened.

Cryptotermes brevis nymphs did not appear to eat or drain the single specimen that died during the course of an experiment. Unlike other species of termites here, they do not seem to eat the exuviae cast during an experiment or in the culture containers. They will drink water if it is offered to them on pieces of paper towel or wood. It appears impracticable to attempt to desiccate them to death, as starvation would probably kill them before drying would.

TABLE IV

DECREASE IN RATE OF WATER LOSS WITH TIME
Rate as Mg/Termite/Hr.

				Rate of Loss at Hour								
Species	Caste	N	Init. Wgt. (mg)	4	12	23	24	48	50	117	119	120
N. castaneus	Nymphs	10	9.55	.245	(allowed to drink; re-weighed, re-run)							
	2nd run	—	9.23	.182	—	.122	—	—	—	—	—	—
	Nymphs	10	9.88	.210	—	—	.141	—	—	—	—	—
	Nymphs	10	10.90	.192	—	—	.128	—	—	—	—	.068
	Nymphs	10	15.02	.367	.290	—	—	—	—	—	—	—
K. jouteli, Wet	Nymphs	10	9.56	.190	—	—	—	.036	—	—	—	.059
	Nymphs	10	10.9	.150	—	—	—	.083	—	—	—	.061
	Nymphs	10	11.04	.107	—	—	—	—	.098	—	—	.061
K. jouteli, Dry	Nymphs	10	14.95	.0675	—	—	.047	—	—	.032	—	—
	NJPM°	—	22.21	.052	(Metamorphosing)		.050	.045	—	—	—	.058
	(8 Imagoes by 144 hours)											
X. schwarzi	Nymphs	10	8.98	.072	—	—	—	.041	—	.032	—	—
	Nymphs	10	11.48	.040	—	—	—	.036	—	—	—	.028
K. snyderi	Nymphs	10	7.87	.045	—	—	—	.023	—	—	.015	—
	Nymphs	10	10.57	.097	—	—	—	.055	—	—	.032	—
C. brevis	Nymphs	10	8.54	No loss	—	—	.007	—	—	—	—	.006

° Nymphs just prior to metamorphosis.

TABLE V

AVERAGE SURVIVAL TIME IN MINUTES AND % BODY WEIGHT LOST AT INTERVALS TO CONSTANT WEIGHT (C. W.) W., S. GROUPS, SPECIES OF *RETICULITERMES*

Species	N	Average Survival Time in Minutes ± S. E.	σ	Av. Init. Wgt. (mg)	Rate of Loss Mg/T/Hr	% Body Weight Lost at 1st death	½ dead	All dead	C. W.
R. hageni	100	266 ± 7.88	78.8	1.12	.151	32.8	55.4	74.7	87.4
R. flavipes	175	326 ± 7.16	94.8	2.73	.259	28.8	47.5	61.2	83.9
R. virginicus	90	369 ± 8.82	84.2	2.53	.181	28.6	42.4	55.5	77.2

TABLE VI

STATISTICAL COMPARISONS, SURVIVAL TIMES FOR SPECIES LISTED IN TABLE V (RATIO OF DIFFERENCE, D TO THE STANDARD ERROR OF THE DIFFERENCE, σD)

Species Compared	$D/\sigma D$	P
R. hageni / R. virginicus	8.65	< .001
R. flavipes / R. hageni	5.33	< .001
R. virginicus / R. flavipes	2.59	.02–.01

Discussion

Survival under desiccation appears to be conditioned by the rate of water loss, body size, and behavior during desiccation. Body size seems to have no relation to rate of loss, but large termites that lose water rapidly may survive desiccation longer than small termites that lose water less rapidly. Termites that remain quiet and grouped during desiccation lose less rapidly than those that are more active. Evacuating the gut upon disturbance, such as removal of the desiccator lid, is probably concerned in the variability in rate of loss in *Kalotermes, Neotermes,* and *Cryptotermes* species. *Reticulitermes* does not seem to give this response so readily.

It has been shown by Kühnelt, Wigglesworth, Ramsay and others that loss of water from the body surface of an insect is prevented or retarded by a layer of fats and waxes, the epicuticle. An additional "cement" layer has been demonstrated in some insects. The presence of protective layers on the termite integument, of differing effectiveness in retarding water loss at 34° C., is suggested by the differences in rate of loss between species, the reduction in rate of loss following exposure to dry air, and the marked differences in rate of loss following culture under very dry, as contrasted to damp, conditions.

It appears unlikely that *Cryptotermes* species and *Kalotermes snyderi* survive in their respective habitats by maintaining a moderate to high humidity within the galleries. Crucial evidence will involve rate of water loss of the eggs, which have not yet been available in sufficient quantity to determine rate of loss. However, it is probable that these species can subsist in dry surroundings on water released from oxidation of food, since the rate of water loss is normally very low and water can be extracted from the digestive wastes before these are voided. Limited observations indicate that a high environmental humidity is detrimental to *Cryptotermes brevis.*

Reticulitermes species require a rather high, constant environmental water supply. While water is not removed from the digestive wastes before voiding, the habits of proctodaeal feeding and using the faeces in constructing protective shelters ultimately result in water conservation. The frequently-observed cannibalistic behavior may also be involved.

Neotermes castaneus and *Kalotermes jouteli* from damp environments lose water rapidly at first, but as desiccation proceeds the rate drops to one near that of other *Kalotermes* species. The large size of both forms, along with the decrease in rate of loss with time, would facilitate survival during intermittent droughts.

Cryptotermes cavifrons, ordinarily an inhabitant of dry, sound wood, has been collected in wood so damp that free water could be forced from it with a knife blade. It will be of interest to determine whether *C. brevis* can survive under such conditions.

No evidence was obtained to substantiate Kofoid's suggestion that the winged forms could survive drying longer than members of the colony lacking the pigmented, rigid integument.

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